Diving behaviour of the Andean frog *Hyla labialis*

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We describe the behaviour of *Hyla labialis* during descent, stationary phase and ascent of voluntary dives in a laboratory tank and in natural ponds. We compare dive times and activity of submerged frogs assigned to six categories established according to developmental stage, gender and reproductive state. In general, the descent took 1.6 % of the total dive time and contained 25 % of the total number of moves per dive, the stationary phase lasted 60.1 % of the total dive time and contained 12.5 % of the moves, and the ascent lasted 38.4 % of the total dive time, with 62.5 % of the moves. The longer the dive, the more moves did a frog make. Among adults, neither gender nor reproductive state was associated with differences in dive time or activity. Juvenile frogs had significantly shorter dive times than adults. The average dive time was significantly longer in a natural pond than in a laboratory tank. Individuals with longer dive times in the laboratory also had longer dive times in the field. Short dive times of juvenile frogs may be associated with their transition from an aquatic to a terrestrial habitat. Reproductive activity was not associated with a prolonged dive time and therefore no particular breath holding capacities seem to be needed for egg laying. A submerged clasping male was not in any conflict situation between sustaining reproductive behaviour and physiological limitations to hold his breath.

INTRODUCTION

The diving behaviour of frogs has received little attention Large inter- and intraspecific variations in dive time may indicate that the decision to immerse and to surface depends on an individual's changing physiological and behavioural state, as well as on life-history aspects and particular external situations (HUTCHISON et al., 1976, PANDIAN & MARIAN, 1985, WEST & VAN VLIET, 1992) Individuals of many frog species spawn in water at a depth that requires complete submergence of the amplectant pair (EIBL-EIBLSFELDT, 1956, DUELLMAN & TRUEB, 1985) and therefore interruption of breathing (ZUG, 1993). A clasping male, carried under water by the female and perhaps depending on her decision to surface, may enter a conflict between his first in priority activity, mating, and his second in priority activity, breathing,

similar to that of the male newt (HALLIDAY & SWEATMAN, 1976) Escaping from predators to an underwater shelter (SCHNEIDER, 1967), as well as diving behaviour involved in foraging activity (GANS, 1969) may also turn into a conflict situation. Thus, dives may be variable in duration because the animal's change in priority depends on several factors.

Reproductively active *Hyla labialis* stay in or near the ponds used for spawning, and dive when disturbed Non-reproductive adults as well as juveniles live an almost entirely terrestrial life away from water bodies (LÜDDECKE, 1995) and cannot avoid predators by diving Therefore, except when being reproductively active and spawning, individuals should show little tendency to dive To determine whether the tendency to dive, diving behaviour and dive time vary according to changes in habitat use and reproductive activity, we performed diving trials with recently metamorphosed juveniles and adult *H labialis* encountered during and between breeding seasons.

MATERIALS AND METHODS

STUDY ANIMALS

All experimental frogs came from 3500 m altitude in the Parque Nacional Natural Chingaza (4°42'N, 73°48'W) Details concerning the area and the collection technique were given elsewhere (LÜDDECKE, 1997). Between August 1996 and May 1997, frogs spent a week or less the laboratory. Frogs to be tested in the laboratory were selected in the field according to criteria related to their developmental stage and reproductive state. Snout-vent length was measured with a calliper to the nearest millimetre and body mass was determined with a laboratory balance to the nearest 0.1 g. We established six frog categories: (J) recently metamorphosed juveniles (*n* = 19); (AM) reproductively active males encountered at the breeding pond and recognised by large and dark thumb pads, dark gular sac, heavy skin secretion and strong odor (*n* = 15), (IM) reproductively inactive males, encountered far from the breeding pond, with small and pale thumb pads and pail throat (*n* = 15), (GF) gravid females, with a body condition index of 80 or more (LÜDDECKE, 1995), oviducts or eggs often visible through the ventral skin (*n* = 15), (SF) spent females, with a body condition index of 70 or less (*n* = 15); and (P) amplectant pairs encountered in the breeding pond (*n* = 5). AM and GF were usually found resting at the pond edge or in the water, whereas J, IM and SF were found away from the pond.

EXPERIMENTAL PROCEDURE

Dive time measurements and behavioural observations were conducted in a glass aquarium 40 × 20 × 80 cm deep which had an internal jacket of plastic mesh 1 × 1 cm It was filled with unaerated water to 4 cm below the rim. Three controlled water temperatures were used. 8, 18 and 28°C, which are within the range of water temperatures experienced in the ponds of *H labialis* (LÜDDECKE, 1995). The experimental temperature to be used was randomly determined for each of the three days (capture day and the following two days) when dive tests were

made For a sequence of three days, each water temperature was used once. The assignment of frogs to temperatures was random Preliminary tests had revealed no significant differences in dive time between frogs used on different days after capture.

In each dive test, a single individual was placed in a plastic tube at the experimental temperature during 30 min prior to a diving event, thus its body temperature equalled the experimental temperature when it was pushed from the tube into the tank at an angle of about 20 degrees to the water surface. This instant marked the beginning of a diving event A diving event ended when the frog had returned to the water surface for breathing. Each individual was submitted at approximately 30-min intervals to three dive tests at the same temperature, carried out on the same evening between 18.00 and 21.00 h local time under artificial light.

Members of amplectant pairs were separated and male and female were first tested independently in the way described above, but only once They were then allowed to clasp again, and the amplectant pair was tested once However, in order to avoid accidental separation, the pair was not introduced into the tube and pushed into the water, but placed gently at the water surface of the tank from where it initiated the dive spontaneously.

Before being released at the capture site in the field, each unmated frog was submitted to one dive test in a natural pond We placed it on a moss cushion at the pond edge, from where it would either jump into the water and dive immediately, or after being touched lightly on its back. Dive time and water temperature at the pond bottom were recorded.

BEHAVIOURAL OBSERVATIONS

Diving frogs were observed continuously from the start to the end of each diving event and their behaviour recorded directly on a record sheet According to preliminary observations, we distinguished three diving phases: descent, stationary phase and ascent. To describe diving behaviour we took into account the mode of locomotion, body postures, changes in head, body and leg position, and diving depth As a measure of a submerged frog's activity we counted its moves. A move could be a small change in body posture, in the position of a leg, or a swimming stroke In each phase we counted all occurrences. Total time of each diving event, and the duration of each diving phase, were determined with a stop watch.

STATISTICAL ANALYSIS

Dive time values of zero (frog did not dive) were excluded from analysis All dive time values were log (x + 1) transformed in order to satisfy criteria for applying parametric tests (ZAR, 1996). ANOVAs were used for comparisons between frog categories Simple and multiple regressions were used to test for associations between temperature, dive time and moves The comparison of field and laboratory dive times was made with a paired t test Data were processed using SYSTAT 5 2 1 for the Macintosh (SYSTAT Statistics, Evanston, III , Systat Inc.). A significance level of $P < 0.05$ was applied in all tests

RESULTS

DIVING BEHAVIOUR

Most frogs dove in all three tests, except for one female and three juveniles. Another two juveniles refused to dive in two of the three tests, and four females, four males and two juveniles refused to dive in one test. Dive time was highly variable, the average for all events of all frog categories except amplectant pairs was 5.04 ± 6.06 min (range: 0.05-46.15 min, $n = 211$), during which a frog made on average 46.6 ± 25.4 moves (range: 1-160 moves, $n = 199$) at an average rate of 14.6 ± 10.9 (range: 1.5-82.7) moves per minute. Frogs dove to the tank bottom in 161 of 211 tests, in 50 tests they came to rest on the tank wall at various depths. At 28°C, we found no dive time difference between 29 tests where frogs came to rest on the tank wall, and 40 tests where they dove to the bottom (ANOVA; 1st event: $P = 0.19$, $n = 24$; 2nd event: $P = 0.69$, $n = 24$; 3rd event, $P = 0.08$, $n = 21$). The diving behaviour of amplectant pairs did not differ from that of unmated frogs. The clasping male seemed to play a passive role during the entire dive. None of the pairs spawned in the dive tank.

Most individuals (96 %) descended with powerful leg strokes while the arms were held backwards against the flanks. Few frogs descended by letting themselves sink. Some frogs initially sank and then swam toward the bottom. After making contact with the plastic mesh, the frog generally moved a short distance on the substrate before becoming stationary, the instant we took to be the end of the descent. On average, the descent took 0.08 ± 0.11 min (range: 0.03-0.96 min, $n = 89$) or 1.6 % of total average dive time, and a frog made on average 25 % of its moves (mean = 10.9 ± 5.1, range: 1-28, $n = 174$).

During the stationary phase, individuals remained at the same depth, most took a sitting or crouching posture and made occasional postural and limb movements and exceptionally short-distance moves. On average, this phase occupied 2.8 ± 2.9 min (range. 0.2-15.0 min, $n = 89$) or 60.1 % of total average dive time, and contained 12.5 % of the moves (mean = 5.4 ± 8.9, range: 1-67, $n = 174$).

The ascent began when the frog, still in a crouched posture, slightly lifted its head. The most common locomotory pattern was walking up the plastic mesh like on a ladder. Most individuals (93 %) ascended slowly by a sequence of alternating moves and halts. Some individuals actively swam to the surface and only a few let themselves float upward. There were also some cases of combining different locomotory patterns. The ascent ended when the frog's nostrils broke the water surface. On average, this phase took 1.8 ± 2.0 min (range. 0.08-10.5, $n = 71$) or 38.4 % of total average dive time, and a frog made on average 62.5 % of its moves (mean = 27.3 ± 15.3, range: 1-144, $n = 174$).

COMPARISON OF SUCCESSIVE DIVING EVENTS OF AN INDIVIDUAL

All frog categories pooled, the first diving event (6.3 ± 7.9 min) was significantly longer than the second and the third (4.7 ± 4.9 min, 4.9 ± 5.4 min, respectively, repeated measures ANOVA, $df = 2$, $P = 0.036$). The difference became more pronounced after excluding juvenile frogs from the analysis (repeated measures ANOVA; $df = 2$, $P = 0.019$). The main reason was

that on average the first diving event of juvenile frogs was the shortest, whereas in the other frog categories the first diving event was the longest (GF, SF, AM and IM pooled; 1st event: 7.2 ± 8.5 min; 2nd event: 5.2 ± 5.2 min; 3rd event: 5.4 ± 5.7 min, for each category separately see tab. 1). We found no differences between the three diving events of all frog categories pooled, neither regarding the number of moves per dive (1st event: 50.9 ± 29.4, $n = 69$; 2nd event: 43.7 ± 22.2, $n = 67$; 3rd event: 44.9 ± 23.5, $n = 63$; ANOVA; $df = 2$, $P = 0.207$), nor the move rate (1st event: 15.7 ± 12.6, $n = 69$, 2nd event: 14.9 ± 11.7, $n = 67$; 3rd event: 13.1 ± 7.9, $n = 63$; ANOVA; $df = 2$, $P = 0.395$).

COMPARISON AMONG CATEGORIES AND GENDER

There were significant dive time differences among frog categories (ANOVAs, all events pooled: $df = 4$, $P = 0.0001$; 1st event: $df = 4$, $P = 0.029$, $n = 58$, 2nd event: $df = 4$, $P = 0.167$, $n = 57$; 3rd event: $df = 4$, $P = 0.017$, $n = 54$), due to juveniles having shorter dive times than adults. After excluding juveniles from analysis, no differences remained between categories (ANOVA; $df = 3$, $P = 0.246$). Thus, although gravid females and reproductively active males tended to dive less time than spent females and reproductively inactive males in almost all diving events at all temperatures, adult males and females had statistically indistinguishable dive times (ANOVAs; all events: $df = 3$, $P = 0.724$, 1st event: $df = 3$, $P = 0.69$, $n = 58$; 2nd event: $df = 3$, $P = 0.259$, $n = 57$; 3rd event $df = 3$, $P = 0.31$, $n = 54$). We found no differences among frog categories regarding the number of moves during the dive (ANOVA; $df = 4$, $P = 0.841$), but significant differences in move rate (ANOVA; $df = 4$, $P = 0.015$), because juveniles had higher rates due to their shorter dive times (tab. 2).

Dive time of amplectant pairs (mean = 6.4 ± 5.2 min, range: 2.4-15.3 min), only measured at the intermediate temperature, did not differ significantly from that in any event of all unmated adult frog categories at that temperature (ANOVAs; $df = 4$ and $n = 43$ in all cases, 1st event: $P = 0.903$; 2nd event: $P = 0.366$, 3rd event: $P = 0.858$). When clasped by a male, the female tended to dive insignificantly longer than when diving by herself (mean = 5.4 ± 3.2 min, range: 1.0-9.5 min; paired t test, $t = 0.33$, $P = 0.759$). The male of mated pairs, diving by himself, had an insignificantly shorter dive time (mean = 1.7 ± 0.5 min, range: 1.2-2.4 min) than the female diving by herself (paired, two-tailed t test, $t = 2.29$, $P = 0.084$), and a marginally significant shorter dive time than when being taken under water by the female he was clasping (paired, two-tailed t test, $t = 2.53$, $P = 0.064$).

RELATIONSHIPS BETWEEN DIVE TIME, MOVES, AND TEMPERATURE

The longer the dive, the more moves did a frog make (fig. 1a). Multiple regression analysis shows that the number of moves was related to dive time (Beta coefficient = 0.41, $P = 0.0001$), but not to temperature (Beta coefficient = 0.04, $P = 0.388$, fig. 2a). Since the number of moves was similar at different temperatures, but dive time shortened at higher temperatures (linear correlation coefficient, $r = 0.46$, $P = 0.0001$, fig. 2b), short dives had very high move rates (fig. 1b). Multiple regression analysis indicates that both, move rate and temperature (fig. 2c), significantly affect dive time (Beta coefficients; move rate: −0.515, $P = 0.0001$, $n = 199$, temperature: 0.346, $P = 0.001$). The positive relation between moves and

Table 1. – Dive time comparison of 75 *Hyla labialis* belonging to five categories, each individual tested three times (events 1, 2, 3) at one of three temperatures. (J) juvenile frogs; (IM) reproductively inactive males; (AM) reproductively active males; (SF) spent females; (GF) gravid females. Sample size (in brackets) refers to number of individuals.

Temperature	Event	J	IM	AM	SF	GF
8°C	1	5.1 ± 6.8 (5)	12.4 ± 13.6 (5)	7.4 ± 3.6 (5)	14.0 ± 18.2 (5)	9.8 ± 4.8 (5)
	2	5.8 ± 4.8 (4)	7.1 ± 6.1 (5)	4.6 ± 1.9 (5)	13.2 ± 11.1 (5)	6.5 ± 2.6 (4)
	3	2.2 ± 4.1 (4)	5.2 ± 2.4 (5)	6.6 ± 3.6 (5)	18.4 ± 12.7 (4)	4.8 ± 2.2 (5)
18°C	1	2.1 ± 1.5 (5)	7.8 ± 5.2 (5)	9.8 ± 11.9 (4)	4.3 ± 2.1 (4)	3.7 ± 1.8 (5)
	2	2.1 ± 1.3 (5)	6.8 ± 5.1 (5)	3.5 ± 2.8 (5)	4.5 ± 2.4 (4)	3.7 ± 1.9 (5)
	3	3.7 ± 3.1 (5)	6.9 ± 4.9 (5)	5.2 ± 2.4 (5)	3.1 ± 2.9 (4)	4.2 ± 1.7 (5)
28°C	1	1.3 ± 0.6 (4)	2.1 ± 1.7 (5)	2.7 ± 1.1 (5)	4.9 ± 4.1 (5)	1.4 ± 0.7 (5)
	2	1.7 ± 1.7 (5)	1.8 ± 1.7 (5)	1.9 ± 1.6 (5)	2.5 ± 1.3 (5)	1.8 ± 0.4 (4)
	3	1.5 ± 1.6 (5)	2.5 ± 0.6 (3)	2.4 ± 0.8 (4)	1.9 ± 0.7 (4)	1.4 ± 0.5 (5)
All temperatures	1	2.4 ± 3.6 (12)	8.4 ± 9.3 (13)	6.7 ± 6.9 (13)	8.9 ± 12.0 (12)	4.8 ± 4.5 (13)
	2	2.6 ± 2.4 (12)	5.9 ± 5.9 (13)	3.3 ± 2.4 (13)	7.7 ± 8.4 (12)	3.9 ± 2.6 (13)
	3	2.8 ± 3.0 (12)	5.2 ± 3.6 (13)	4.9 ± 3.1 (13)	7.8 ± 10.4 (12)	3.6 ± 2.2 (13)

Table 2 – Dive time and activity comparisons of 75 *Hyla labialis* belonging to five categories, including all three events and all three temperatures. (J) juvenile frogs; (IM) reproductively inactive males; (AM) reproductively active males; (SF) spent females; (GF) gravid females. Sample size refers to the number of dives.

Frog category	n	Dive time (min)	Number of moves	Moves per minute
J	31	3.7 ± 3.6	45.7 ± 28.3	19.1 ± 14.9
IM	43	6.0 ± 6.3	46.8 ± 28.1	12.7 ± 9.1
AM	43	4.8 ± 4.5	50.4 ± 28.6	15.0 ± 11.7
SF	39	7.7 ± 9.8	45.7 ± 25.9	10.8 ± 7.8
GF	43	4.1 ± 3.3	44.2 ± 15.4	16.2 ± 10.1

dive time is mainly due to the ascent, which contained 62.5 % of the moves, and less to the descent and the stationary phase, which contained only 25 % and 12.5 %, respectively, of the total number of moves.

FIELD OBSERVATIONS

None of the frogs tested in the field tried to escape by moving away from the pond. All frogs dove to the bottom of the pond and usually entered the soft layer of mud where they were invisible to observers. They reappeared at the beginning of the ascent, when they lifted their head out of the mud, usually close to where they had entered. They remained for up to several minutes in this position, before they continued the ascent by leaving the mud and
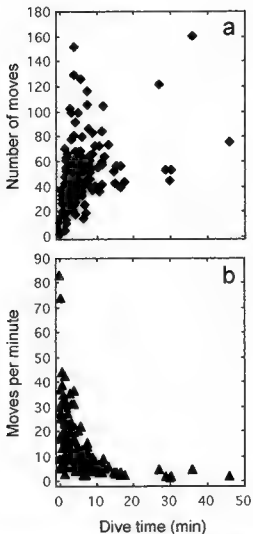
Fig. 1   Relationships between dive time in the laboratory, number of moves during a dive, and rate of moves, in *Hyla labialis*. All events included

swimming to the surface, or by first walking some distance on the mud surface and then slowly climbing up aquatic plants.

There were no significant field dive time differences among frog categories (ANOVA, $df = 4$, $P = 0.069$), even though juvenile frogs had rather short, and reproductively inactive males had rather long dive times. Pooled dive times for all categories at corresponding temperatures (using the laboratory record for low or intermediate temperatures closest to the temperature of each frog diving in the field) were significantly longer in the field (8.9 ± 6.6 min) than in the laboratory (6.5 ± 5.8 min, two-tailed paired t test, $df = 37$, $t = 3.27$, $P = 0.002$). Individual field and laboratory dive times were significantly and positively correlated for all individuals (linear correlation coefficient, $r = 0.74$, $P = 0.0001$, $n = 37$), and also within each of three (SF, AM, J) of five categories (fig. 3).
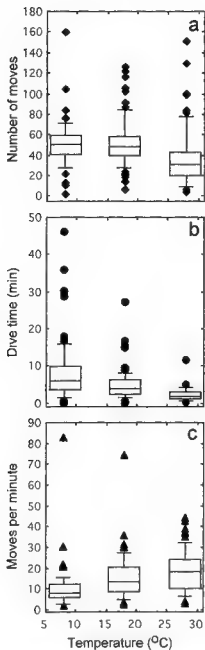
Fig 2   Relationships between water temperature dive time in the laboratory number of moves during
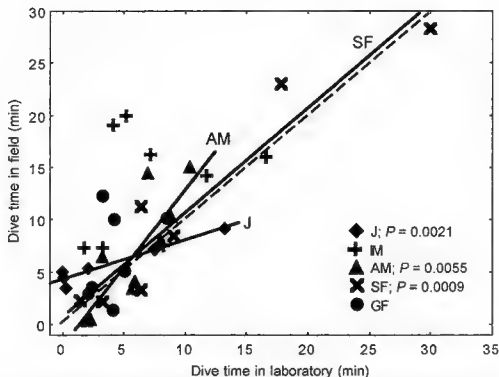a dive, and rate of moves, in *Hyla labialis* All events included

Fig 3   Relationship between dive times in the laboratory at 8 or 18°C, and in a natural pond at 9-16°C, of 37 *Hyla labialis* belonging to five frog categories. Diagonal traced line indicates dive times of equal duration. Continuous lines are regression lines for three frog categories.

DISCUSSION

Since frogs sun basking on a moss cushion at the pond edge plunged into the water when disturbed, diving was assumed to be a protective behaviour against terrestrial predators. In this context, the function of the descent is to take the frog down fast and efficiently by actively swimming towards the bottom. The relatively long lasting and passive stationary phase also indicates that a frog dives to escape, particularly since in a natural pond the diver usually penetrates into the mud layer at the bottom of the pond, where it is visually concealed. Finally, lifting the head and looking upward before beginning to ascend, as well as the frequent halts of the frog on its way up, could be interpreted as vigilance by visually screening the surroundings for predators across the totally transparent water of these natural ponds. According to our procedure, we assumed that the frogs would perceive the push into the water as a predator attack, and expected dive time and behaviour to be related to the risk. If risk were related to body size, then juvenile frogs should dive longest. This expectation was not fulfilled. Alternatively, since a frog probably ignores a predator's persistance in waiting for it to surface, its antipredator strategy may as well be to surface at an unpredictable moment

(BAIRD, 1983). Further, despite the difference in procedure, amplectant pairs showed the same behavioural diving patterns and similar dive times as did unmated frogs, which suggests that the predator-simulating push did not have much influence on dive time.

The high variability of dive times suggests that changes in behavioural priorities are involved (HALLIDAY & SWEATMAN, 1976). For instance, juvenile *H. labialis* are in transition to a terrestrial lifestyle, thus the lower tendency to dive and shorter dive times of metamorphosed frogs may be associated with avoidance of a high predator risk in the aquatic habitat (WILBUR & COLLINS, 1973; WASSERSUG & SPERRY, 1977; SKELLY, 1994). Reproductively active frogs may terminate a dive in order to continue mate searching, which is done at the water surface. The exceptionally short dive times of males of pairs, diving by themselves after having been separated from the female, may reveal restlessness motivated by searching for the missing mate.

The rather paused return to the surface suggests that *H. labialis* begin to ascend long before depleting their oxygen stores. Although an urge to breathe is unlikely to be second in priority, physiological aspects may play a role in diving behaviour. For instance, the negative correlation between underwater activity and dive time of *H. labialis*, also found in other amphibians (HALLIDAY & WORSNOP, 1977), is associated with temperature, and together they may determine when threshold levels of blood oxygen concentration are reached (HUTCHISON et al., 1976; BOUTILIER, 1990). Since unmated males had dive times similar to those of pairs, we assume that a male clasped to a submerged female is not in any conflict between holding on to her or breathing. Apparently, spawning behaviour does not rely on particular breath holding capacities, because the time spent submerged for spawning seems to be very short in most anuran species (see WEYGOLDT & POTSCH, 1992). The tendency to dive may also be associated with temperature preferences or individual experiences. Although *H. labialis* is thermophilic (VALDIVIESO & TAMSITT, 1974; LÜDDECKE, 1995), the unfamiliar experience to descend into a warm depth may be the reason for a reduced tendency to dive to the bottom of the tank at high water temperatures, since in nature it would always find cooler temperatures as it dives deeper. Finally, since an individual frog tended to make either longer or shorter dives, irrespective of place and time of day, performance differences among individuals may be due to inherent physiological or behavioural properties.

ACKNOWLEDGEMENTS

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